

ISSUES , IDEAS  
AND  
INFORMATION  
FOR PSYCHOLOGY  
STUDENTS

NO.4 - ANIMAL  
BEHAVIOUR

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# **1. CALIFORNIA GROUND SQUIRRELS AND DECEPTIVE COMMUNICATION**

- 1.1. Introduction
- 1.2. Visual deception
- 1.3. Olfactory deception
- 1.4. References

## **1.1. INTRODUCTION**

Prey develop tactics of defence against predators. The California ground squirrel (*Spermophilus beecheyi*) (figure 1.1) has to defend its pups against northern Pacific rattlesnakes (*Crotalus oreganus*) (figure 1.2) and Pacific gopher snakes (*Pituophis melanoleucus*) (figure 1.3) among other predators. The tactics that have evolved include being resistant to rattlesnake venom and so able to confront and harass the predator (Poran et al 1987). Particular strategies are used with snakes (table 1.1).



(Source: Franco Folini)

Figure 1.1 - California ground squirrel.

## STRATEGY

- Tail flagging
- Resistant to venom
- Substrate throwing - loose stones and dirt
- Harassment by many animals
- Acoustic signals not used (only with birds and mammals)

Table 1.1 - Strategies used against snakes by ground squirrels.



(Source: Rebou)

Figure 1.2 - North Pacific rattlesnake.

### 1.2. VISUAL DECEPTION

One strategy used by ground squirrels is tail flagging - the side to side motion of the erected tail. It has been found that this is a deceptive visual signal to rattlesnakes. Blood flowing to the tail makes it erect, but it is also warm. Heat gives off infrared radiation, and infrared sensitivity is used by rattlesnakes. Thus the tail flagging in infrared appears as a larger animal confronting the rattlesnake.

Rundus et al (2007) established this information experimentally<sup>1</sup>. Infrared video recording of twelve adult female ground squirrels during interactions with snakes in the laboratory showed tail infrared emissions during encounters with rattlesnakes (that use infrared), but not with gopher snakes (which do not use infrared). In the latter case, the tail was wagged without heat. Faced with rattlesnakes, the tail temperature was significantly higher (26-28°C) compared to other situations - gopher snakes, other squirrels, and baseline (23-25°C).

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<sup>1</sup> Film of experiment at <http://www.pnas.org/content/104/36/14372/suppl/DC1>.



(Source: Antendrus)

Figure 1.3 - Pacific gopher snake.

Rundus et al built a biorobotic squirrel model to simulate the tail flagging behaviour. The two robots used were constructed from taxidermic models of California ground squirrels and impregnated with squirrel odour. One model produced tail flagging behaviour, and the other heated tail wagging. Both robots were heated to 31°C to mimic body temperature.

Tail flagging caused the fourteen adult rattlesnakes to become more cautious, and infrared tail flagging even more so (eg: remained still longer, and in a coiled position). The snakes also took longer to enter the simulated burrow: average 35.1 minutes in infrared compared to 4.1 minutes (baseline - no squirrel present).

### **1.3. OLFACTORY DECEPTION**

In another example of deception, Clucas et al (2008) found that California ground squirrels and rock squirrels (*Spermophilus variegatus*) chew on skin shed by rattlesnakes and lick their pups to give the odour of the rattlesnake (which uses smell to hunt). This behaviour can be seen in the context of animals using the resources

in their environment as in tool use.

Chewing shed snake skin and licking their fur, known as "snake scent application" (SSA), was first reported in Siberian chipmunks (*Eutamias sibericus asiaticus*) (Kobayashi and Watanabe 1986).

The "self-application" or "anointment" with foreign substances is used with different species for varying reasons:

- Anti-predator defence - to smell like the predator and thus will not be attacked.

The desire to mask their own smell is supported by the application of scent to the posterior of the body where the anal glands are the major source of odour. Clucas et al (2008) found significantly more licks to that area of the body after chewing the snake skin.

- Ectoparasite defence - to smell and taste unpleasant to parasites; eg: birds bite millipedes and apply to feathers (Parkes et al 2003).
- Conspecific deterrence - smelling like a predator deters members of own species from the area, and reduces competition for mates/food, and/or repels infanticidal conspecific females.
- Infiltration disguise - eg: beetles cover themselves with dead ants so they can integrate into ant colonies without attack (Vandermeer and Wojcik 1982).
- Social bonding - eg: wolves roll on prey carcass (Zimen 1981).
- Reason unclear - eg: grey squirrels roll around on ants and ant hills (Hauser 1964).

Clucas et al (2008) tested three hypotheses for the motivations of SSA. Only the anti-predator hypothesis was supported by the data (table 1.2).

Hypothesis-testing is a key element of science. The researcher makes a prediction, based on previous research, about what is expected to happen. The experiment is then designed to establish if the hypothesis is correct. Often competing hypotheses are tested to see which prediction is supported by the data.

An untested hypothesis was that SSA alerts other animals to the presence of a predator in the area. Thus it is a form of genuine predator warning communication.

REASON	PREDICTION	FINDINGS
Anti-predator defence	Juveniles and adult females will SSA more than adult males because young most vulnerable to rattlesnake attack. (Females lick their pups)	SUPPORTED  Juveniles and adult females engaged in twice as much SSA as adult males (mean SSA duration: 200 vs less)
Ectoparasite defence	Juvenile California ground squirrels will SSA more than adults because they have more fleas	NOT SUPPORTED  Juveniles engaged in more SSA than adults males, but not adult
Conspecific deterrence	i. Adult males will SSA more to gain an advantage for mates with rival males  ii. This difference will be more pronounced in California ground squirrels because male-male aggression greater in	NOT SUPPORTED  i. Adult males less SSA than juveniles and adult females  ii. No difference in SSA between adult males of both species

Table 1.2 - Three hypotheses tested for SSA and findings from Clucas et al (2008).

During the experiment, a shed skin of the local rattlesnake species was laid out three metres from an active burrow. The California ground squirrels were studied at Lake Solano Country Park, California, and the rock squirrels at Caballo Lake State Park, New Mexico, USA.

The squirrels' reaction towards the snake skin was videotaped, and later analysed. A pilot study with trial videos checked that the experimental procedure was feasible and appropriate. The final results were based upon thirty California ground squirrels (14 adult females, 9 adult males, 7 juveniles) and 41 rock squirrels (16 adult females, 14 adult males, 11 juveniles).

Clucas et al performed video analysis of SSA in two ways:

i) Frame-by-frame - to measure total number of licks to each body location, and then calculated the proportion of licks to that body area. Event recording counts the number of times a behaviour occurs;

ii) Real-time - to measure total amount of time spent applying scent (in seconds). Time samples lasting thirty seconds were used.

Video-recording of animal behaviour has many

advantages for the researchers compared to human observers, but it is not perfect (table 1.3).

#### ADVANTAGES

1. Records behaviour without selection bias or subjectivity.
2. Allows later frame-by-frame analysis to avoid missing details.
3. Frame-by-frame analysis allows detailed analysis of the behaviour beyond the human eye with, for example, slow motion.
4. Ideal for situations where too much is happening for observers to see all.
5. Digital cameras can be clearer and more accurate than human vision.
6. Camera can be left for very long periods unattended which is not possible with human observers.
7. Trial videos allow researchers to test behaviour categories, practise using them, and establish inter-observer reliability.

#### DISADVANTAGES

1. Can only record behaviour in area of camera's view, whereas humans can look around as required.
2. Depends upon the quality of the equipment, and thus the images produced.
3. Unforeseen technical problems, and equipment can be affected by weather, light, and animals.
4. Depends upon where camera(s) set up if stationary, or, if carried, the skill of the camera operator.
5. Human observers can make decisions on the spot concerning what is important.
6. Researchers still need to interpret what is happening.
7. Some aspects of behaviour cannot be video-recorded, like smell.

Table 1.3 - Advantages and disadvantages of video-recording animal behaviour compared to human observers.

Because the data were non-normally distributed, Clucas et al had to use non-parametric inferential statistics tests, like the Mann-Whitney U Test for differences between two groups (table 1.4).

The Mann-Whitney U test compares the central tendency of two independent samples (table 1.5).

TWO GROUPS	U VALUE	LEVEL OF SIGNIFICANCE
* Adult males vs adult females SSA duration	191.0	0.005
* Adult males vs juveniles SSA duration	94.0	0.002
* Adult males SSA duration: California ground vs rock squirrels	54.5	0.332 ns
* Adult females SSA duration: California ground vs rock squirrels	104.0	0.550 ns

(ns = not significant)

Table 1.4 - Examples of results from Clucas et al (2008) using Mann-Whitney U test.

#### ADVANTAGES

1. Shows the significant difference between two sets of data.
2. Straightforward to calculate, and can be done by hand with small samples.
3. Does not need normally distributed data as parametric inferential statistics tests do.
4. Can be used with ordinal data, whereas parametric tests should not be.
5. Works well with samples of different sizes.
6. It deals with the relative positions not absolute scores by ranking the data (Coolican 1990).
7. Does not require equal numbers in each group.

#### DISADVANTAGES

1. Not as efficient at finding significant differences between the sets of data as parametric tests like the t-test.
2. Typical of non-parametric tests, it is less sensitive than parametric tests to the data collected.
3. More risk of type I or type II errors than with parametric tests.

4. Not as effective if many tied ranks.
5. Technically it is not an alternative to the t-test (Hart 2001).
6. Can be affected by differences in the spread of data (Hart 2001).
7. Converting all data to ranks can lose some of the detail of interval/ratio data (ie: ordinal data does not have equal distance between each number on the scale).

Table 1.5 - Advantages and disadvantages of Mann-Whitney U test.

SSA behaviour has advantages and disadvantages for squirrels (table 1.6).

#### ADVANTAGES

1. Mask their smell from predators.
2. Effective because snakes use smell in hunting.
3. The behaviour followed a similar stereotyped sequence, "typically beginning with the flank and progressing to the tail tip" (p304); "chewing the shed skin, twisting to the side and licking the flanks, grabbing the tail with forepaws and then licking along the length of the tail from base to tip" (Clucas et al 2008 p302). It is also observed in other rodent species. These suggest an evolutionary basis to the behaviour, developed from the grooming pattern.

#### DISADVANTAGES

1. Risk of attack if mistaken for snake.
2. May not be effective and snake not deceived.
3. Side effects and risks of chewing shed snake skin.

Table 1.6 - Advantages and disadvantages of SSA by squirrels.

## 1.4. REFERENCES

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## **2. AN EXAMPLE OF A PHYSICAL INTERVENTION STUDY WITH RED GROUSE**

- 2.1. Introduction
- 2.2. Evaluation of study
- 2.3. Presentation of data
- 2.4. References

### **2.1. INTRODUCTION**

Male red grouse (*Lagopus lagopus scoticus*) (figure 2.1) are a highly territorial bird, whose level of aggression in defending that area is linked to levels of testosterone. Redpath et al (2006) artificially varied the levels of testosterone in autumn (territory establishing period) to see the effect. High levels of testosterone has both evolutionary benefits and costs for a male animal (table 2.1).



(Source: Roger Butterfield)

Figure 1.1 - Red Grouse.

BENEFITS	COSTS
1. Increased competitive success for territory. 2. Increased competitive success for breeding. 3. Increased attractiveness to mates through physical appearance changes in secondary sexual characteristics (eg: size of grouse comb). 4. Increased productivity in terms of fathering offspring. 5. Better chance of mating with	1. Increased exposure to predators through aggression and conspicuousness. 2. Increased risk of injury from fights. 3. Susceptibility to disease and parasites as testosterone suppresses the immune system. 4. Loss of physical condition. 5. Increased testosterone during chick-rearing has negative impact on parental care.

Table 2.1 - Benefits and costs of high levels of testosterone in males.

123 males from six sites in the UK were used in the experiment. Half (n = 64) were given three-month active testosterone implants (which produced artificially high levels of the hormone), and the others (n = 59) an inert implant (ie: no substance released). During the period of the research, September to April, the birds were checked five times to see who had survived and who had paired with a female in the spring.

Less of the males with testosterone implants (56%) survived until the spring compared to 70% of the controls. The former group were more likely to be predated by raptors (birds of prey) and less likely by mammals like stoat and badgers.

Almost all surviving testosterone implanted males (90%) had paired with a female by the spring compared to about two-thirds of the control group. The former group fathered an average of 2.4 young compared to 1.4.

Artificially high levels of testosterone helped the birds to find and keep the better territory, and thus the opportunity for mating, but it increased the risk of death from aggressive behaviour with other males and with predator birds.

## 2.2. EVALUATION

1. The birds were caught individually at night by dazzling them with a powerful torch rather than with large nets which could risk injury or death.

2. The birds were fitted with radio tracking devices

which aided the process of finding the birds again, particularly at night or in poor visibility, compared to wing tags. The devices weighed only about 2% of the animal's body weight. Radio tracking devices do not effect grouse survival (Thirgood et al 1995).

3. The birds were randomly allocated to the experimental or control group.

4. The birds were changed by having an implant and a radio tracking device. The implants (20mm long) were placed under the skin of the flank with local anaesthetic. Tests with captive birds found no adverse effects of the operation.

5. Because different sites were being studied at the same time, there were periods between visiting each site. One upshot was that the cause of nineteen of 46 mortalities could not be established.

6. Putting an implant into experimental and control birds standardised the procedure.

7. This study was a physical intervention experiment which involved attempting to change the behaviour of the animal through a physical change. It allows manipulation of variables to test a hypothesis that is not possible with naturalistic observation, but the animals are artificially changed. There are also ethical concerns about such studies, like whether it is right to interfere in such a way.

### **2.3. PRESENTATION OF DATA**

Table 2.2 summarises the number of grouse used from each of the six sites, and how many died (or were lost) during the study. The general finding, as mentioned above, was that testosterone implanted males were more likely to die.

It is important how the data are presented and summarised, particularly because different methods of summary can give different impressions about the results. The most straightforward visual presentation of the data can be a bar-chart. This shows clearly that more testosterone implanted males died in total and as a percentage (figure 2.2).

SITE	TYPE OF IMPLANT	TOTAL NUMBER OF MALES USED	NUMBER DIED/LOST	PERCENTAGE DIED/LOST
1	I	19	8	42.1
	T	21	9	42.9
2	I	4	1	25.0
	T	6	3	50.0
3	I	8	2	25.0
	T	7	3	42.9
4	I	10	3	30.0
	T	9	4	44.4
5	I	9	1	11.1
	T	11	7	63.6
6	I	9	6	66.7
	T	10	5	50.0
<b>TOTAL</b>	<b>I</b>	<b>59</b>	<b>21</b>	<b>35.6</b>
	<b>T</b>	<b>64</b>	<b>31</b>	<b>48.4</b>

(I = inert; T = testosterone)

(After Redpath et al 2006 Table 2 p1299)

Table 2.2 - Summary of data from six sites.

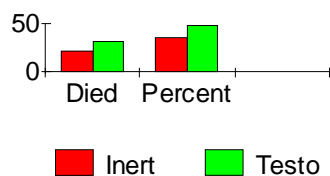


Figure 2.2 - Bar-chart to show number and percentage of males who died during study.

The data can be summarised in terms of the average or measure of central tendency, and depending upon which is used, a different figure is produced (table 2.3).

MEASURE OF CENTRAL TENDENCY	INERT IMPLANT	TESTOSTERONE IMPLANT
Mean	3.5	5.2
Median	2.5	4.5
Mode	1	3

Table 2.3 - Three measures of central tendency for data in table.

Each measure of central tendency has advantages and disadvantages (table 2.4). The mean is probably the best for these data, though the median can be helpful. The mode is of little use here.

MEASURE OF CENTRAL TENDENCY	ADVANTAGES	DISADVANTAGES
Mean - Add up the scores and divide by number of scores	1. Total and all values taken into account. 2. Most sensitive.	1. Can violently change because sensitive. 2. Not good if extreme scores (outliers) or scores
Median - Middle number when numbers ranked or halfway between middle two if even	1. Shows exact middle point with 50% above/below. 2. Unaffected by extreme values in one	1. Does not take into account exact value of each item. 2. Time consuming to rank large sets of
Mode - Most common score	1. Score obtained most often. 2. Unaffected by extreme values in one	1. Does not take into account exact value of each item. 2. Crude measure.

Table 2.4 - Key advantages and disadvantages of the three measures of central tendency.

## 2.4. REFERENCES

Redpath, S.M et al (2006) The effects of autumn testosterone on survival and productivity in red grouse, *Lagopus lagopus scoticus* Animal Behaviour 71, 1297-1305

Thirgood, S.J et al (1995) Effect of necklace radio transmitters on survival and breeding success of red grouse Wildlife Biology 1, 121-126

### **3. USE OF ROBOTS IN ANIMAL EXPERIMENTS**

- 3.1. Introduction
- 3.2. Example: use with house finches
- 3.3. References

#### **3.1. INTRODUCTION**

"Robot animals" can be used to interact with animals to "test particular predictions of animal behaviour" (Webb 2000). Usually models are built that look like the animal they are imitating, and specific behaviours can be programmed. The aim is to make the robots "life-like".

There are a number of advantages and disadvantages of studying animal behaviour using robots summarised in table 3.1.

#### **ADVANTAGES**

1. Allows manipulation of variables that would otherwise be dependent on live animals producing (eg: visual cues). It is possible to control the physical appearance and movement of robot animals.
2. Researchers can test hypotheses without interfering with live animals physically (eg: robot animals with enlarged body parts).
3. Can be used in difficult situations (eg: trying to manipulate behaviour of flock or group).
4. Better than 2D stimuli like pictures or static fibre glass models.
5. Using live animals to act as senders of messages is affected by the responses of receivers.
6. Not affected by environmental variables (eg: weather, predators).
7. No problems of keeping as with live animals.

#### **DISADVANTAGES**

1. Not the same as live animals.
2. Most robots are programmed with specific behaviours and cannot adapt to the response of live animals.
3. Live animals may be able to tell that not real, for example, by the smell.
4. Real animals may habituate to robots and not respond because of limited behaviours of robots. In Fernandez-Juricic et al's experiment (see later), the birds habituated to the robot's behaviour in nine minutes on average.
5. Cost of building the robot.

6. Live animals may be using cues to behaviour or communication not recognised by researchers, and thus not programmed with the robot.
7. Difficult to programme robots to do a lot of different behaviours, so usually limited to single behaviour patterns (eg: head movements).

Table 3.1 - Advantages and disadvantages of using robot animals to study animal behaviour.

### 3.2. EXAMPLE: USE WITH HOUSE FINCHES

Fernandez-Juricic et al (2006) built robot birds to study the social foraging of house finches (*Carpodacus mexicanus*) (figure 3.1). Social foraging is where animals find food together, and has the advantage that some individuals can watch for predators while others eat.

Two models of house finches were built (male and female) that could move their heads up and down to give the impression of eating (head down) or watching for predators (head up).

The house finches did respond to the robots as if real birds. For example, when the robot had its head up, the real birds consumed more seeds than when the robot's head was down. In other words, when one bird is watching for predators (in this case the robot), the other birds eat.

### 3.3. REFERENCES

Fernandez-Juricic, E et al (2006) A dynamic method to study the transmission of social foraging information in flocks using robots Animal Behaviour 71, 901-911

Webb, B (2000) What does robotics offer animal behaviour? Animal Behaviour 60, 545-548



(Source: Mathew Hunt (Coneslayer))

Figure 3.1 - Male house finch.

## **4. THE EXPERIMENTAL STUDY OF VISUAL IMPRINTING**

- 4.1. Introduction
- 4.2. Bolhuis et al (2000)
- 4.3. References

### **4.1. INTRODUCTION**

Early learning in a number of species of precocial bird (eg: ducks, chicken) occurs through filial imprinting (Lorenz 1937). Filial imprinting is an instinctive process of attachment, though it is classed as learning because it is not entirely automatic. For example, a chick follows the first thing it sees <sup>2</sup> after hatching or a certain time after hatching (critical period); this is instinct, but what that involves is the learning part.

This mechanism of imprinting has been tested experimentally by rearing chicks in darkness and only showing them certain visual objects. The chick is tested for preference by presenting the imprinted visual object or a neutral stimulus. For domestic chickens (*Gallus gallus domesticus*), the chick is placed on a running wheel which records the rotation if the animal moves towards an object. A preference score of 100% would mean the chick always approached the imprinted (previously seen) object, and 0% that they approached the never-seen object all the time (Bolhuis et al 2000) <sup>3</sup>.

Over the years many different visual objects have been tested for imprintability. This included a rotating black-and-white disc, a flashing light, a moving box, and adults of other species (Sluckin and Salzen 1961) as well as Konrad Lorenz himself with goslings.

In recent years, chicks have been divided into "good learners" (preference score >65%) or "poor learners" (preference score <65%) in these experiments to establish any physiological differences between them; eg: neurochemical (McCabe and Horn 1988) or genetic (McCabe and Horn 1994).

---

<sup>2</sup> Imprinting can occur with senses other than vision, like olfactory and auditory.

<sup>3</sup> Bolhuis et al (2000) defined the preference score in their research as "number of quarter rotations of the running wheel as chick attempted to approach the training stimulus" divided by "total number of quarter rotations of the running wheels towards each of the stimuli" times 100 (p1155).

#### 4.2. BOLHUIS ET AL (2000)

Bolhuis et al (2000) were interested to explore more about the differences between good and poor learners in imprinting experiments among domestic chickens. Over 100 eggs were hatched in darkness, and maintained in darkness (or dim green light which has no effect on imprinting) unless being tested.

At 24 hours after hatching the chicks were individually presented with a rotating red box or a rotating blue cylinder as the visual stimulus in bright illumination for thirty minutes while a maternal call was played. Then the chicks were given a preference test for their stimulus and the unseen one. The chicks were assigned to High or Low preference groups based on this test.

The next day half of each group received extra training and the others did not. All chicks received another preference test (figure 4.1).

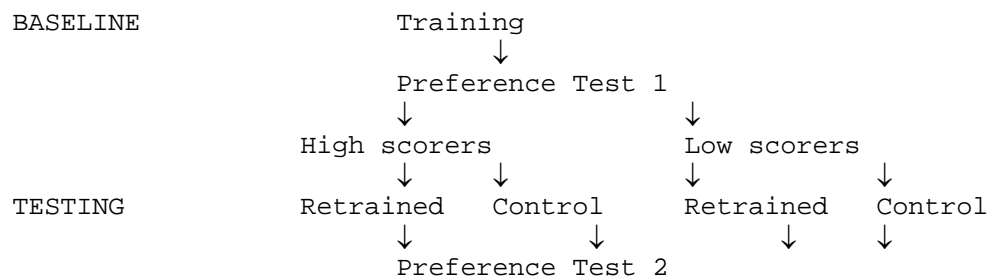


Figure 4.1 - Design of experiment by Bolhuis et al (2000).

The laboratory experiment allows the researcher greater control over the variables, animals, and the environment than naturalistic studies. Table 4.1 gives some examples of the experimental controls used by Bolhuis et al (2000).

- Same breed of chicks ("Ross 1")
- Constant temperature for hatching (37.5°C)
- Standardised procedure for newly-hatched; eg: 6-10 hours after hatching moved to individual compartments maintained at 34°C
- Handling chicks avoided as much as possible because of potential effects on imprinting
- Testing at standardised times (24 hours after hatching) and for standardised periods (eg: 45 minutes)
- Control chicks at retraining exposed to experimental situation with overhead light only while retraining group being shown visual stimulus

Table 4.1 - Examples of experimental controls used by Bolhuis et al (2000).

The mean preference score (PS) significantly improved for the retrained chicks in the Low group (from 55% to over 70%). The other groups did not change their PS between the preference tests.

Bolhuis et al (2000) then replicated the study but varied the retraining - (a) retraining on same day as learning, (b) three periods of retraining, and (c) four periods of retraining. In all three cases the chicks in the Low group showed significant improvements with retraining.

The results showed that some chicks are quicker learners than others. The quick learners will immediately follow what they see after hatching or during the critical period (presumably the mother). This makes evolutionary sense, whereas the slow learners take time to imprint and this is risky. But if the quick learners imprint on to something that is not the mother, there is a disadvantage to such behaviour. So slow learners, taking time to imprint, may have an advantage in some cases.

Imprinting as a form of learning has a number of advantages and disadvantages for the chick (table 4.2).

#### ADVANTAGES

1. It is instinctive behaviour that occurs immediately or soon after hatching which does not require reinforcement.
2. Allows for some basic learning like the object to imprint on to - the ability to discriminate familiar from unfamiliar. An instinctive "concept" that requires experience to "flesh it out" (Lea 1984).
3. In animals mobile immediately after hatching/birth, there is a risk of them wandering off. An automatic response to follow reduces this risk.
4. Where many offspring, imprinting aids the mother in controlling them (ie: they just follow her).

#### DISADVANTAGES

1. Not very sophisticated behaviour which can be easily tricked as in imprinting experiments.
2. If imprinting occurs with the wrong object, it is virtually irreversible.
3. The exact physiological mechanisms of imprinting has not been established.
4. The critical period during which imprinting occurs varies between species.

Table 4.2 - Advantages and disadvantages of visual imprinting.

#### 4.3. REFERENCES

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## **5. HOMING TO NATAL SITE FOR REPRODUCTION**

- 5.1. Salmon
- 5.2. Navigational cues
- 5.3. References

### **5.1. SALMON**

Homing involves migration back to a natal site (place of birth) for reproduction after feeding migrations (Quinn et al 2006). One commonly studied group of animals are the family Salmonidae (salmon, trout, and charr).

Quinn et al (2006) studied the homing behaviour of sockeye salmon (*Oncorhynchus nerka*) (figure 5.1) in a stream (Hansen Creek) off Lake Aleknagik in Alaska, USA. Embryos from 28 female and 25 male salmon of that area were marked.

The sockeye salmon emerges in Hansen Creek, migrates to Lake Aleknagik to feed for a year, then migrates to sea for two more years of feeding. They return to Hansen Creek to breed and spawn at age four years before dying.



(Source: US Fish and Wildlife Service)

Figure 5.1 - Sockeyed salmon.

Quinn et al sampled the dead salmon in Hansen Creek for those marked four years earlier. Statistically more marked animals returned to the natal site than would have been expected by chance.

Homing to the place of birth has a number of advantages and disadvantages for the animal (table 5.1).

ADVANTAGES	DISADVANTAGES
1. A specialist site for breeding.  2. Move to food when not breeding.  3. Know where to find mates in geographically dispersed	1. Energy required to travel.  2. Navigational problems of finding natal site again.  3. Problems of remembering location of breeding site.

Table 5.1 - Advantages and disadvantages of homing to natal site to breed.

## 5.2. NAVIGATIONAL CUES

It is believed that salmon use olfactory cues to return to their place of birth. These are the odours of the local geology and flora which were imprinted during incubation (Quinn et al 2006).

Animals use different types of cues or combinations of these cues to navigate (table 5.2).

VISUAL CUES
<ul style="list-style-type: none"> <li>landmarks</li> <li>cognitive maps</li> <li>position of sun</li> <li>polarised light - reflection of sun on water</li> <li>position of stars</li> </ul>
MAGNETIC CUES
CHEMICAL/OLFACTORY CUES
SOUND

Table 5.2 - Types of cues used by animals to navigate.

One means of finding the right direction to travel in homing is a "magnetic compass". This is a sensitivity to the earth's magnetic field (which varies around the globe) and the animals use to orientate themselves.

Wiltschko and Wiltschko (1972) showed the "magnetic compass" in night-migrating European robins (*Erithacus rubecula*) in captivity. If magnetic North was artificially moved, the birds changed their direction of heading also.

Wiltschko and Wiltschko (1972) then showed that the "magnetic compass" in robins was not based on the polarity of the magnetic field (ie: in relation to magnetic North), but was based on the inclination of the magnetic field in space.

Further research has shown that the magnetoreceptors in robins were sensitive to certain types of light as well as changes in magnetic wavelength (Wiltschko and Wiltschko 1999).

Other birds that have a "magnetic compass" (up to twenty species) are migratory except for the carrier pigeon (*Columba livia*) and the domestic chicken (*Gallus gallus*) (Wiltschko et al 2007).

Wiltschko et al (2007) studied the "magnetic compass" in 36 chicks reared in isolation using a standard experimental procedure. The testing arena was a square white pen with white screens that allowed only light through, but no visual objects (which could aid orientation). The arena was oriented to magnetic North.

The chicks were trained to find a red ball hidden in one particular direction, with an equal number of chicks trained to North, South, East and West. Then they were tested in a situation where magnetic North had been moved ninety degrees clockwise to the East by means of pairs of Helmholtz coils. The chicks were between 12-22 days old.

If the chicks had learned the location of the red ball using the magnetic field, they would hunt for it at ninety degrees clockwise.

The strength of the magnetic field was also varied. Creating a magnetic field that was weaker or stronger than the local geomagnetic field (experiments in New South Wales, Australia) produced disorientation in the chicks.

Though chickens do not migrate, the fact that they possess a "magnetic compass" similar to migrating birds suggests "that this type of compass is of great age and probably was already developed in the common ancestors of all modern birds" (Wiltschko et al 2007).

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## **6. FATAL FIGHTING**

- 6.1. Fatal fighting in birds
- 6.2. Reasons for fatal fighting
- 6.3. References

### **6.1. FATAL FIGHTING IN BIRDS**

Animals of the same species come into conflict over territory and mates (contested resources), mainly. Fatal battles are risky, because death means the loss of many years of potential breeding for long-living animals, so strategies have evolved where animals can assess each other to avoid conflict, or where the conflict is limited. However, fatal fighting has been observed in certain species (eg: some spiders over territory; Piper et al 2008).

Piper et al (2008) were interested in exploring the routine occurrence of fatal battles among common loons (*Gavia immer*)(figure 6.1). These large diving birds were observed in 98 breeding territories in Wisconsin, USA <sup>4</sup>. Males control the nest placement, but nest-building, incubation of eggs, and caring for offspring for first eleven weeks are joint activities. Adult pair members remain physically close which aided observation. Territory is acquired in three ways (table 6.1).

TERRITORY ACQUISITION	MALE	FEMALE
• Passive replacement of dead resident	21	23
• Pairing in vacant breeding space	28	30
	51	47

Table 6.1 - Three ways territory acquired based on sex (%).

Territorial take-over, where the owner is displaced, and the winner breeds with the displaced residents' mate occurs for both sexes. This was an average of 2-4 territorial intrusions per day in the breeding season, of which 23% of those observed ended in physical fights.

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<sup>4</sup> This is a well-studied population since 1993 during which most loons were marked with coloured leg bands.



(Source: US Federal Government employee)

Figure 6.1 - Common loon.

Two kinds of aggressive behaviour were recorded:

- "Low-level aggression" - the resident chasing an intruder out of their territory.
- "Overt fighting" - physical contact including grabbing the opponent's head with the bill and beating with the wing.

It was found that males were more aggressive than females, and received more injuries and death from aggression. Based on observations of fights and number of birds subsequently missing, it was estimated that the frequency of male fatal battles was between 16-33% of all fights. No females were found dead from fights. These figures are estimates because the losers in fights who disappeared were not all found. Some may have migrated early, or moved to other lakes, or died from other causes like predation.

Other studies that have examined carcasses of dead loons in other areas found injuries consistent with fatal fights (eg: bill spearing in 20% of Minnesota sample; Pichner and Wolff 2000).

## 6.2. REASONS FOR FATAL FIGHTING

Why do these birds engage in fatal fights because there is no shortage of breeding opportunities with many unpaired adults and abandonment common? One possibility is the reproductive benefits to good territory which the individual birds remember and return to each year (site familiarity).

Another explanation is that the resident males who fight to the death are older, and so have less ability to move to a new territory and find another mate, as females

tend to stay in the territory and not follow displaced males. This is known as low "residual reproductive value" (RRV)(Williams 1966) - they stand little chance of moving elsewhere and breeding successfully there in the event of displacement" (Piper et al 2008 p1113).

Piper et al (2008) offered two other possible reasons for fatal fights. Firstly, the males are unable to assess their likelihood of winning contests and so keep fighting until it is fatal. Other species overcome this risk by evolving honest signals of body size and condition to aid the assessment of winning a fight.

For example, male red deer (*Cervus elaphus*)(figure 6.2) engage in "ritualised fighting" involving roaring contests and parallel walking to assess each other. Only 20% of observed approaches by two males in the breeding season ended in actual fights (Clutton-Brock and Albon 1979).



(Source: Heinz Seehagel)

Figure 6.2 - Male red deer.

The other reason that common loons fight to the death could be that after an initial injury, the loser cannot escape and is doomed to repeated attacks that

prove fatal. Piper et al felt that this is plausible because loons struggle to fly (often running 100 metres across the water to take-off). Any injury to the wings will make this even harder.

Table 6.2 summarises the possible reasons for fatal fights.

REASON FOR FATAL FIGHT	RESIDENT	INTRUDER
• Good territory hard to find	yes	yes
• Low RRV	yes	no
• Unable to assess when to stop	yes	yes
	yes	yes

Table 6.2 - Possible reasons for fatal fights in relation to residents and intruders.

### 6.3. REFERENCES

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## **7. DIFFERENCES IN EVOLUTIONARY BEHAVIOUR:** **FEMALES ACTING LIKE MALES - POLYANDRY**

- 7.1. Introduction
- 7.2. Polyandry
- 7.3. Sequential polyandry
- 7.4. Constraints on polyandry
- 7.5. References

### **7.1. INTRODUCTION**

In many species, males compete to impress females, and then, often, mate with multiple partners. But there are situations where the sex roles are reversed.

In the theory of sexual selection (Darwin 1871), males and females of a species have different reproductive costs which produce differences in evolution (sexual dimorphism). As Charles Darwin originally noted:

..sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species . . The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners (Darwin 1871 p614 quoted in Clutton-Brock 2009 p3).

This difference is most evident in secondary sexual characteristics, primarily in males. These are characteristics that indirectly improve a male's chance of mating, and include "weapons" (eg: antlers) to defeat other males or "ornaments" (eg: bright colours) to attract females.

Much of the focus has been upon male secondary sexual characteristics, but females in many species also have such characteristics to aid their competition with other females and for access to males (Clutton-Brock 2009). The different situations include:

- Females competing against females in groups where only the dominant females mate each year.
- Females competing against females in polyandrous

species (eg: female soay sheep (*Ovis aries*) have horns).

- Females competing for access to males in species like the seahorses (*Hippocampus subellongatus*) where males brood eggs. Females have evolved larger body size than males. Male mating preference will drive evolutionary changes in females to show that they have "good genes".

Overall, Clutton-Brock (2009) believed that the evolution of secondary sexual characteristics were different between the sexes: "Because of their greater energetic investment in gametes and parental care, females more commonly compete with each other for access to resources necessary for successful reproduction (including breeding sites, parental care and social rank) than for access to gametes produced by the opposite sex" (p7).

## **7.2. POLYANDRY**

Polyandry is most common in fishes (eg: pipefishes *Syngnathidae*) and birds (eg: shorebirds *Charadrii*) that lay eggs.

Maklakov and Lubin (2006) felt that it was "clear that males will increase their reproductive success by mating with multiple females. But, the benefits to females of multiple mating are not so obvious" (p31).

Andersson (2005) explained the evolution of polyandry based on:

i) Males caring for the eggs (and offspring) without the assistance of the female;

ii) Females being able to lay more eggs than a single male can accommodate. For example, in moorhens (*Gallinus chloropus*) females with plenty of food can produce a new batch of eggs before the male has finished caring for the first clutch, so she needs another male;

iii) Females compete with each other to lay eggs with different males.

Crucial to the development of polyandry is the evolution of male uniparental care. There are a number of possibilities for how the male caring for the eggs and young by themselves evolved in different species (Andersson 2005):

a) Egg production is demanding for the female bird who needs to spend much of her time feeding and has

little time for parental care;

b) High risk of the whole clutch or nest being lost, so females spend time in preparing a replacement (eg: building another nest, producing more eggs), and males care for the current nest;

c) In some fishes, female fecundity increases with age, and so spending time caring for the current batch, instead of feeding, limits opportunities for greater number of offspring in the future. While for males, fecundity reduces with age, and so it is better to care for the offspring now than worry about the future ones.

Among shorebirds, females can become polyandrous because they precede males to the nesting areas and wait for the intermittent arrival of males. So a female mates with the first male who arrives at the nest, raises this clutch (or the male does), and then mates with a later arriving male (Schamel et al 2004).

Polyandry can occur against the female's best interests where males force, seduce or manipulate females to mate with another male (Clutton-Brock and Parker 1995). This is particularly the case in species where mating involves the risk of physical injury, like some spiders.

Maklakov and Lubin (2006) investigated a species of spider where the female can both mate with multiple males but also resist it. Spiders (*Stegodyphus lineatus*), collected in the Negev Desert in Israel, and studied in the laboratory were divided into single mated (SM), double-mated with two males (DM), or single-mated but rejected second male (RE). The amount of food available was varied in the experimental conditions.

An indirect benefit for polyandry was found in female offspring from the DM group having a larger body mass under a low-food condition. This was not the case for male offspring or in the high-food condition.

An indirect benefit is a benefit to the genes of the individual rather than to the individual themselves (direct benefit). Having larger offspring means that the mother's genes are more likely to survive in subsequent generations (increased offspring viability benefits). This compensates for the direct costs of mating (eg: males who stay on female's web after mating reduces female's opportunity for food and she loses weight).

### **7.3. SEQUENTIAL POLYANDRY**

Sequential polyandry is where females mate with multiple males in one breeding season.

There are a number of reasons proposed for this behaviour which is spreading the risks of (Byrne and Keogh 2009):

- Mating with an infertile male (fertility insurance hypothesis);
- A poor father (paternal care hypothesis);
- Poor quality male genes (intrinsic male quality hypothesis);
- Genetically incompatible male (genetic incompatibility hypothesis);
- Nest failure in an unpredictable environment, where males provide the nest. In these species, females are dependent on the nests provided by males and have to assess their quality along with the quality of the male offering the nest. The quality of nest is linked to survival of offspring.

Byrne and Keogh (2009) tested this last explanation for polyandry among the Australian toadlet *Pseudophryne bibronii*. Females lay their eggs in terrestrial nests constructed by males, and it is males who stay with the developing eggs. The nest has to have a certain level of soil moisture. Also when the nest is flooded, to allow the tadpoles to swim away, is crucial, but the females can have no control over this. It is related to the arrival of the rains. Ultimately, there is a high risk of loss of brood before maturity.

A population of 53 males and 48 females from an area in Jervis Bay National Park, North South Wales, Australia were studied. Parentage of eggs were established genetically from the sixty-two of the 71 nests where eggs were laid. Females divided their eggs between five nests on average (range 2-8 nests). The more nests used by the females, the significantly greater mean offspring survivorship (table 7.1).

NUMBER OF NESTS	MEAN TADPOLE SURVIVORSHIP
2	35
5	50
7	55

Table 7.1 - Mean tadpole survival based on number of nests where females laid eggs.

Females mating/laying their eggs with up to eight males is quite an extreme case of polyandry as the figure

is less in other species where the behaviour occurs (eg: up to four males in shorebirds; Byrne and Keogh 2009). But the risk of brood loss is very high for these toadlets. For example, 30 nests had 50% survival or less, of which half of these had less than 20% of the average 118 eggs laid surviving. On the other hand, 22 nests had 80% survival or greater. Not only is the risk of loss high, but the females cannot know in advance which nests will be the most successful because of the unpredictability of flooding and drought.

So females laying the eggs in multiple nests is the evolutionary most beneficial strategy, but the downside for females is increased risk of predation and disease contraction, and increased energy expended.

A simple mathematical example can show the benefits of multiple nest laying compared to single nest laying (table 7.2). If the survival rate is always the same, the polyandry with five males is always advantageous until scenario no.4 in the table. In species where females do not care for the eggs after laying, and do not make nests, sequential polyandry has evolved as the best strategy to maximise survival of offspring.

SCENARIO	EGGS SURVIVING IN SINGLE NEST LAYING	EGGS SURVIVING IN FIVE NEST LAYING	BEST STRATEGY
1. 50% survival	50	$50 \times 5 = 250$	Polyandry
2. 50% survival vs 25% survival in multiple nests	50	$25 \times 5 = 125$	Polyandry
3. 50% survival vs 10% survival in multiple nests	50	$10 \times 5 = 50$	No difference
4. 50% survival vs 5% survival in	50	$5 \times 5 = 25$	Single nest

Table 7.2 - Mathematical examples of egg-laying strategies with 100 eggs.

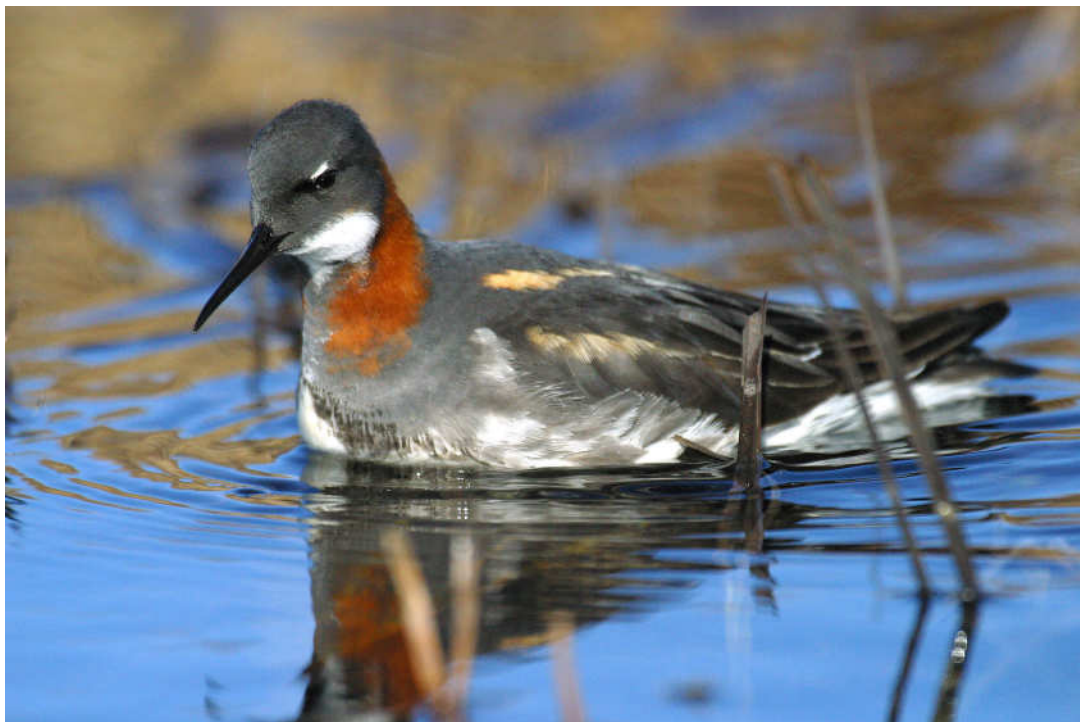
Table 7.3 lists the main advantages and disadvantages of polyandry.

ADVANTAGES	DISADVANTAGES
1. Spread risk of loss of brood from single mating with infertile, incompatible or poor quality male. 2. Spreads risk of loss of brood after eggs laid. 3. Best strategy where females leave after egg-laying/mating. 4. Benefits from multiple "nuptial gifts" in species where males provide them.	1. Increased energy expended in multiple mating/egg-laying. 2. Increased risks of predation, disease and dehydration, and less time for foraging. 3. Increased risk of physical injury during mating, particularly in female coerced. 4. No guarantee that other females will not lay eggs in same nest, nor that male who owns nest will fertilise eggs (eg: 10 of 53 males "sneaking fertilisations" of other males' nests; Byrne and

Table 7.3 - Main advantages and disadvantages of sequential polyandry.

#### 7.4. CONSTRAINTS ON POLYANDRY

Sequential polyandry will be constrained by certain factors, and Schamel et al (2004) tested them among red-necked phalaropes (*Phalaropus lobatus*) (figure 7.1) nesting at Cape Espenberg in Alaska, USA.



(Source: US Fish and Wildlife Service)

Figure 7.1 - Red-necked phalarope.

Polyandry will be limited by:

- a) The female's ability to produce more and good quality eggs after the first clutch;
- b) The availability of males;
- c) The male's desire to avoid polyandrous situations.

The first possibility was not relevant as female red-necked phalaropes produce the same mean clutch sizes (3-4) in the first and second clutches. In fact, eggs in their second clutch of the breeding season were significantly larger than the first clutch.

Males provide all parental care, so their availability for females to mate again is important. Schamel et al found no relationship between number of males available (through clutch failure) and female polyandry.

The male's desire to re-nest with their original mate after clutch loss, which was 66%, limited the female's opportunities for polyandry. If the original female was not available, many of the males left the area or failed to re-nest. The motivation of the males was to decrease the risk of caring for eggs fertilised by another male. If a male finds a new female, she may be storing another male's sperm from a previous mating, and the current male cannot know if his mating produced paternity for the eggs he will care for.

Part of sexual selection is an evolutionary battle between the male and female of the species over the best strategy. For females of this species of birds, it is polyandry, but for the males it is closer to monogamy. There are costs and benefits for each sex here (table 7.4).

MATING STRATEGY	MALES	FEMALES
POLYANDRY	Cost: caring for eggs did not father	Benefit: multiple nests spread risk of clutch loss
MONOGAMY	Benefit: know he is father	Cost: if clutch lost no offspring that breeding

Table 7.4 - Costs and benefits of polyandry and monogamy for males and females.

The "evolutionary battle of the sexes" can be seen in a female's willingness to mate with the same male again. Zeh et al (1998) found that female pseudoscorpions (*Cordylochernes scorpiodes*) rejected the previously mated male offered again shortly after mating, but not if a

long period of time had elapsed.

Fifty-four female pseudoscorpions from the Republic of Panama were studied in the laboratory. The females were allowed to mate with a male, and then presented with the same male (SM) or a different one (DM) 1.5 hours and 48 hours later (two different experiments). Table 7.5 summarised the findings which were significant for 1.5 hours ( $p = 0.0002$ ; Fisher's exact test).

Males wanted to mate at every encounter, whereas females were choosy. "Just as sexual selection may be better understood as a process in which males compete not for females themselves but for access to females' gametes.. so too may sexual selection be viewed as a process in which females choose not males themselves but rather the sperm which will fertilize their eggs" (Zeh et al 1998 p13736).

	SAME MALE (SM)	DIFFERENT MALE (DM)
1.5 hours between matings	15.4	69.2
48 hours between	53.8	69.2

(After Zeh et al 1998)

Table 7.5 - Percentage of females accepting sperm in second mating.

The males' willingness to mate with the same female is an attempt to reduce post-copulatory sexual selection (eg: sperm removed by subsequent male), while the females' selectivity encourages sperm competition (ie: the "best" sperm from multiple mates fertilises the egg).

## 7.5. REFERENCES

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## **8. THE BENEFITS OF CANNIBALISM OF OFFSPRING BY THE MOTHER**

- 8.1. Introduction
- 8.2. Maternal cannibalism
- 8.3. Intra-uterine cannibalism
- 8.4. References

### **8.1. INTRODUCTION**

Parental care and filial cannibalism (consumption of own offspring by parent) are found together in the same species; for example, bank vole (*Clethrionomys glareolus*) and house finch (*Carpodacus mexicanus*) mothers, and both parents of the burying beetle (*Nicrophorus orbicollis*) (Klug and Bonsall 2007). It can be whole-clutch or partial-clutch.

Filial cannibalism appears to be a trade-off between current and future reproductive success of the parent(s) in a number of ways (Klug and Bonsall 2007):

- Where food is short, eating the offspring gives the parent(s) energy to survive and have the opportunity for future reproduction (energy-based hypothesis);
- Where there are many offspring in the nest, eating the lower-quality offspring benefits both the parent(s) and the better-quality offspring (density-dependent egg survivorship);
- The removal of offspring may make a parent attractive to mates, particularly if good-quality mates now available.

### **8.2. MATERNAL CANNIBALISM**

Maternal cannibalism is the eating of either the "non-viable offspring (eggs, undeveloped ova or stillborn neonates) or of living offspring" (Mociño-Deloya et al 2009).

The consumption of non-viable offspring in a litter could be the mother's attempt to protect the viable offspring through removing chemical cues that might attract predators or preventing the spread of disease to healthy offspring. This benefits the living offspring.

Alternatively, maternal cannibalism could benefit the mother by providing energy without the need to forage. Of course, both explanations may be correct (Mociño-Deloya et al 2009).

Studying Mexican lance-headed rattlesnakes (*Crotalus polystictus*), Mociño-Deloya et al (2009) made the following predictions:

i) If maternal cannibalism benefits the living offspring first and foremost, it should be more common when a high proportion of the litter are viable (parental care hypothesis);

ii) But if it benefits the mother primarily, maternal cannibalism will occur when many offspring are non-viable, the mother is in a poor condition following egg-laying, or there is less time to forage or food available (maternal recovery hypothesis).

Stillborn neonates are similar to live offspring in that they are motionless after birth, so the female has to be careful in deciding to consume a neonate. Eating undeveloped ova is less risky.

Females snakes along the Rio Lerma in Mexico were captured and studied in cages over three breeding seasons (May to mid-August). It was found that 68% (63 of 93) post-parturient (after egg-laying) females ate some or all their non-viable offspring. But not all non-viable offspring were eaten - 17% of cannibals did not eat all available. The researchers accepted that the capture of the snakes may have had an effect.

Females who cannibalised offspring did not show a preference between undeveloped ova and stillborn neonates (as analysed with 2 x 2 contingency X2 test; table 8.1).

Number of females who ate ova	Number of females who ate stillborn
Number of females who did not eat	Number of females who did not eat

Table 8.1 - Categories in a 2 x 2 contingency X2 test like the one used by Mociño-Deloya et al (2009).

The X2 statistical test compares the observed frequencies of a behaviour to those expected by chance (table 8.2).

Using an independent student's t-test, there was no significant difference in time that females waited to cannibalise in litters containing stillborn neonates than litters without (mean 21.5 vs 18.7 hours). So the risk of consuming live (immobile) neonates did not seem a concern.

ADVANTAGES	DISADVANTAGES
<p>1. No restriction on type of data used.</p> <p>2. Versatile and can be used in different ways (eg: test of difference and "goodness of fit" test).</p> <p>3. Easy to use.</p> <p>4. One of the few tests for categorical/nominal data.</p>	<p>1. Need a minimum number of observations: not less than five for expected values in less than 20% of cells (Coolican 1990).</p> <p>2. Care in interpreting significance because it shows difference to chance not necessarily difference in direction predicted.</p> <p>3. If sample is less than 25 or expected value less than 10 in any cell, it requires the Yates' correction (Coolican 1990). This makes the <math>\chi^2</math> smaller and reduces the risk of a type I error.</p> <p>4. Each observation must be independent and mutually</p>

Table 8.2 - Advantages and disadvantages of  $\chi^2$  statistical test.

The data seemed to support the maternal recovery hypothesis because snakes cannibalised non-viable offspring when there were many of them in the litter, and when the females gave birth later in the year (when food in short supply).

Support for the maternal recovery hypothesis comes from another species of snake. Lourdaïs et al (2005) observed Colombian rainbow boas (*Epicrates cenchria maurus*) maintained in the laboratory. They found that females who ate non-viable offspring to the equivalent of half the litter mass recovered from pregnancy faster. This recovery was shown in significant improvements to:

- Climbing ability - when held by the tail, speed to reach handler's hand;
- Escape from predator - strength of reaction to handler stretching out body;
- Prey handling - greater muscle strength to consume prey.

These behaviours relate to survival and foraging, and cannibalism of non-viable offspring gave the females energy benefits to overcome the energy costs of reproduction and pregnancy.

### 8.3. INTRA-UTERINE CANNIBALISM

Indirect benefits to the mother can occur through another type of cannibalism - intra-uterine. This is where the most-developmentally advanced embryo(s) in the womb eat the remaining embryo(s), or eat the unfertilised eggs (the latter is known as oviphagy). This occurs in the grey nurse shark (*Carcharias taurus*) where there is no placental connection between the mother and the embryo(s), and the offspring are born ready to fend for self as not parental care. There are usually two embryos (one in each uterus) (Otway et al 2003).

The indirect benefit to the mother is in the survival of her genes through the better-quality offspring, with no energy cost of feeding during pregnancy or afterwards.

### 8.4. REFERENCES

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## **9. ANIMAL BEHAVIOUR WEB TASKS: LEARNING AND GENETICS**

Here are three ideas to search the Internet and find information related to animal behaviour topics. The websites listed are starting points only, and are not claimed to be comprehensive.

### **1. Classical and Operant Conditioning and Training Dogs**

Dogs are usually trained with rewards and punishments. These are examples of processes in operant conditioning. Find out how they are applied in training police dogs by the Royal Canadian Mounted Police Dog Service ([http://www.rcmp.ca/pds/index\\_e.htm](http://www.rcmp.ca/pds/index_e.htm)).

See also (<http://101-dog-training-tips.com>) and how to sites in no.3 below.

### **2. Genetics and Selective Breeding of Racehorses**

The process of inheritance of traits can be seen through selective breeding. One animal that has been specially bred over many generations is the thoroughbred racehorse. Go the site of one company that specialises in this process to find out about the genetics involved (<http://thoroughbredgenetics.com/index.html>)

See also (<http://www.bloodlines.net/TB>) and general information on heritability estimates (<http://extension.missouri.edu/xplor/agguides/ansci/g02910.htm>).

### **3. Observational Learning, Modelling and Learning New Skills**

Find a video demonstration of a new skill and look for principles of modelling and imitation by the "teacher" (<http://www.ehow.com>), (<http://www.videojug.com>) and (<http://www.expertvillage.com>).

## **10. A BRIEF EARLY HISTORY OF COMPARATIVE PSYCHOLOGY**

- 10.1. The beginnings
- 10.2. Four key researchers of the twentieth century
- 10.3. References

### **10.1 THE BEGINNINGS**

Comparative psychology is a sub-division of psychology that involves the study of non-human animal behaviour to understand human behaviour. However, some comparative psychologists argue that animal behaviour should be studied for its own sake.

This is the first of a number of debates that originated in the late nineteenth and early twentieth century as psychology and comparative psychology were developing and they still continue today (Dewsbury 2000).

Another debate relates to the methodology used. Kinnaman (1902) distinguished five methods:

- Free observation of animals in their natural environment (naturalistic observation);
- Developmental study - studying the animal from birth to adulthood and onwards;
- Animal training - as used by many Behaviourists with rats in mazes, for example;
- Free observation of animals in captivity (controlled observation);
- Laboratory experiments.

Then there is the question of which animals to study with these methods. The laboratory rat was the most popular subject from the 1920s onwards for a large part of the twentieth century (Dewsbury 2000).

Evolution was a relatively new idea in 1900 and the understanding of the concepts were limited (compared to the knowledge today). How humans fitted into evolution created divisions at the time. For example, Wilhelm Wundt (1902) saw humans as no different to other animals in substance: "the mental life of animals shows itself to be throughout, in its element and in the general laws governing the combination of the elements, the same as the mental life of man" (p308; quoted in Dewsbury 2000 p751). While others, like G. Stanley Hall and James Rowland Angell, saw a gap between humans and non-human animals.

This division was also evident in the "higher abilities" (eg: consciousness, reason) attributed to non-human animals (eg: Romanes 1882) or not (eg: Loeb 1912).

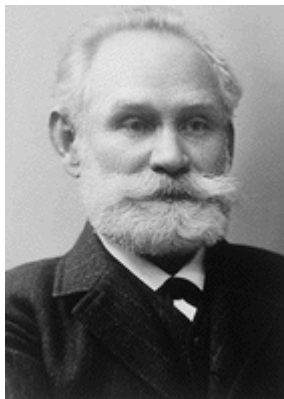
The attempt to resolve such disagreements has shown itself in projects to teach human language to apes, beginning with the chimpanzee, Peter (Witmer 1909) and continuing to the present with work like that of Sue Savage-Rumbaugh (eg: Savage-Rumbaugh et al 1998).

Thankfully some earlier ideas in comparative psychology have disappeared, like Yerkes's (1911) belief that plants had some form of conscious mind.

## 10.2. FOUR KEY RESEARCHERS OF THE TWENTIETH CENTURY

It is difficult to reduce the many studies and researchers down to just four, but the contribution of these individuals to comparative psychology (and psychology generally) are the most important because of the key concepts they introduced and the amount of time spent on their work.

- Ivan Pavlov (eg: 1927)(figure 10.1) - Work with dogs on learning and established the principles of classical conditioning.



(Source: Public domain)

Figure 10.1 - Ivan Pavlov.

- Konrad Lorenz (eg: 1935)(figure 10.2) - Work on the principles in early imprinting in geese, in particular. His ideas underpin ethology.
- J.B Watson (eg: 1924 <sup>5</sup>) - Most famous for his application of classical conditioning to humans in the case of "Little Albert" (Watson and Rayner 1920).

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<sup>5</sup> Examples of publications available at <http://psychclassics.yorku.ca/author.htm#l>.

- B.F Skinner (eg: 1938 <sup>6</sup>) - Work with, primarily, pigeons, and rats, to establish the principles of learning by operant conditioning.



(Source: Public domain)

Figure 10.2 - Konrad Lorenz.

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<sup>6</sup> Examples of publications available at <http://psychclassics.yorku.ca/author.htm#l>.

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